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POPULATION ECOLOGY OF THE NORTHERN SPOTTED OWL (*Strix occidentalis caurina*) IN NORTHWESTERN CALIFORNIA: ANNUAL RESULTS, 2001

CONTRACTOR

University of Minnesota
St. Paul, MN 55108

PRINCIPAL INVESTIGATORS

Dr. Alan B. Franklin
Colorado Cooperative Fish & Wildlife Research Unit
Colorado State University
Fort Collins, CO 80523

Dr. R. J. Gutiérrez
University of Minnesota
Department of Fisheries and Wildlife
St. Paul, MN 55108

RESEARCH FELLOWS

Peter C. Carlson
University of Minnesota
Department of Fisheries and Wildlife
St. Paul, MN 55108

David Pavlacky
University of Minnesota
Department of Fisheries and Wildlife
St. Paul, MN 55108

RESEARCH SPECIALISTS
Jeremy Rockwiett, Wendy King, Abe Walston, and Shem Unger

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INTRODUCTION

The northern spotted owl (*Strix occidentalis caurina*) is closely associated with old-growth Douglas-fir (*Pseudotsuga menziesii*) forests on public lands in northwestern California (Gould 1974, Gutiérrez et al. 1984, Solis and Gutiérrez 1990, Sisco 1990, Blakesley et al. 1992, Hunter et al. 1994, Franklin et al. 2000). Logging of these old-growth forests was considered to be a major factor in the decline of spotted owl populations which subsequently led to the listing of this species as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1990). Recently, Franklin et al. (2000) found that ecotones between older forest and other habitats may be additional important components of northern spotted owl habitat in northwestern California.

Basic demographic data has been useful for assessing the present and future status and management of spotted owl populations (see Burnham et al. 1996). Our study was initiated in 1985 as long-term study on the population dynamics of northern spotted owls with the primary objectives of:

1) Estimating life-history parameters such as reproductive output, annual survival, and longevity.

2) Assessing the effects of environmental variation (such as habitat configuration and climate) on life-history parameters.

3) Estimating rates of change in the population over time; and

4) Understanding population behavioral and regulatory mechanisms.

Information has been collected and disseminated for all these objectives. This report provides additional information on estimates and trends in life-history parameters and population rates of change for the northern spotted owl in northwestern California. In this report, we used a different approach in estimating rates of population change than in previous reports (e.g., Franklin et al. 2001) because of problems in estimating juvenile survival using mark-recapture estimators. In the new approach we used a reverse-time mark-recapture estimator developed by Pradel (1996) and further refined by Nichols and Hines (2002). In addition, we also relied on a random-effects modeling approach to examine trends in both survival and rates of population change (Franklin et al. 2002). In past reports, we had used this approach only in estimating reproductive output.

STUDY AREA

We studied spotted owls in two areas of northwestern California (Figure 1): a regional study area (RSA) and the Willow Creek Study Area (WCSA). The RSA encompassed approximately 10,000 km^2 (3,861 mi^2) and included portions of the Six Rivers, Klamath and

Shasta-Trinity National Forests and lands administered by the U.S. Bureau of Land Management. The area actually surveyed for northern spotted owls within the RSA was approximately 1,784 km^2 (688 mi^2).

The Willow Creek study area (WCSA) encompassed 292 km^2 (113 mi^2) and was located just south of Willow Creek, Humboldt Co., California in the central portion of the RSA. The WCSA was selected originally in 1985 for intensive study because (1) the study area was easily delineated by geographic boundaries, (2) the history of occupation by spotted owls was well known through previous surveys and research, and (3) the area was accessible by roads. The WCSA is managed primarily by the Lower Trinity Ranger District, Six Rivers National Forest with a small portion managed by the Big Bar Ranger District, Shasta-Trinity National Forest. Elevations ranged from 200 m (650 ft) to 1700 m (5580 ft).

Climate within the study areas is characterized by cool, wet winters and hot, dry summers. The dominant land use in the WCSA was timber production with clearcutting being the principal method of logging. However, logging declined, and then ceased, on public land within our study areas over the course of the study. The vegetation was Mixed Evergreen, Klamath Montane, Oregon Oak and Tan Oak forest types (Küchler 1977). Additional description of the climate, physiography, and vegetation of the study area was presented by Franklin et al. (1986). Six vegetative cover types occurred on the WCSA; four represented different seral stages of coniferous forest (CF) (Franklin et al. 1990b, Hunter 1994). These cover types were described as follows: CF1 - nonvegetated or grass and forbs associated with seedling conifers <2.5 cm diameter at breast height (dbh); CF2 - brush associated with sapling conifers ranging from 2.5-12.6 cm dbh; CF3 - pole and medium conifers ranging from 12.7-53.2 cm dbh; CF4 - mature and old-growth conifers ≥53.3 cm dbh; HDW - hardwood trees comprising >80% of basal area; and Water. Based on analysis of LANDSAT imagery, 35.3% of the WCSA was covered by CF4, 12.8% by CF3, 14.4% by CF2, 8.9% by CF1, 28.3% by HDW and 0.3% by Water (Hunter 1994).

METHODS

We attempted to locate and identify all individual spotted owls in the WCSA and on selected territories in the RSA. Territories in the RSA were selected based on where spotted owls were banded during previous studies (e.g., Gutiérrez et al. 1985) and to provide a wider geographic sample for estimating demographic parameters. spotted owls were located using vocal imitations of their calls to elicit responses (Forsman 1983). Individuals were identified by initial capture, marking and subsequent recapture or resighting colored leg bands. Most of our methods were either adapted from Forsman (1983) or developed during previous research projects (Gutiérrez et al. 1984; Gutiérrez et al. 1985; Franklin et al. 1986, Franklin et al. 1990b). Methods for recording data collected in the field were described in Franklin et al. (1986, 1996).

Surveys

Both day and night surveys were used to locate spotted owls. Night surveys were conducted between dusk and 0200 hours (Pacific Standard Time) and consisted primarily of point surveys. A minimum of 10 minutes was devoted to each call station during point surveys. Day surveys were used to locate roosting owls and consisted of walk-in surveys and cruise

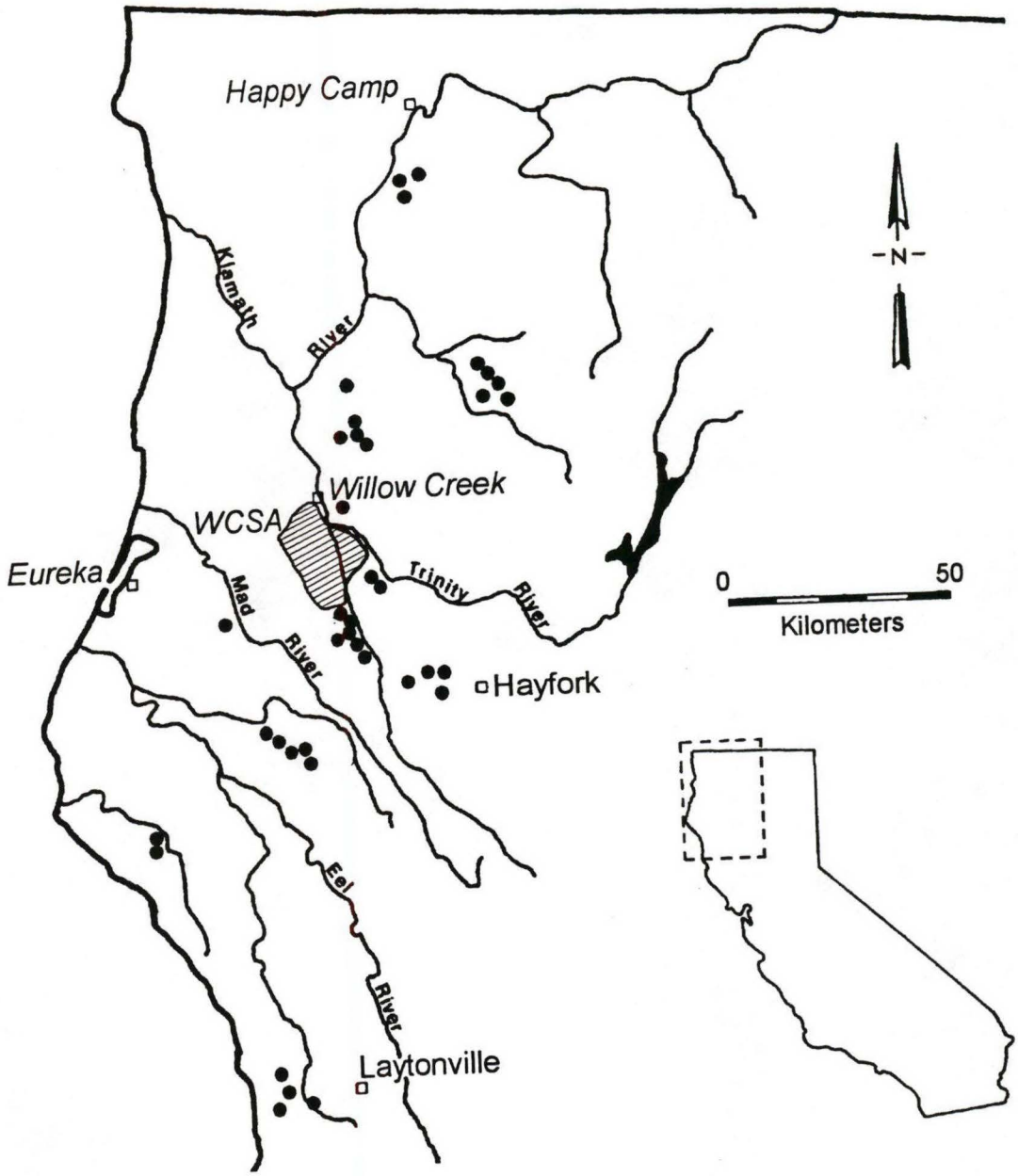

Figure 1. *Map of northern spotted owl territories (dots) surveyed in the Regional Study Area, northwestern California. Shaded area represents the Willow Creek Study Area.*

surveys. Walk-in surveys were initiated during the day at sites where owls had been located previously. Cruise surveys were 1) conducted in habitat considered potentially occupied, or areas presumed occupied based on night surveys and 2) conducted in areas known to contain owls but where no owls were detected during the survey. The two types of surveys differed in that walk-in surveys were successful in detecting owls whereas cruise surveys were unsuccessful in detecting owls.

Once located, owls were checked for reproductive activity by feeding live mice to individuals (Forsman 1983). Breeding spotted owls take prey and fly to the nest or fledged young; non-reproductive owls either eat or cache the mice. Lack of reproductive activity was inferred if (1) an owl took ≥ 2 offered mice, and cached the last mouse taken, (2) a female did not have a well-developed brood patch during the incubation period, or (3) a combination of the above 2 criteria. We attempted to visit owls at least twice during the sampling period to determine the number of fledged young or to confirm lack of reproductive activity. Reproductive activity of each owl visited was characterized as having 0, 1, 2, or (rarely) 3 fledged young. A territory was assumed unoccupied if spotted owls were not detected after five night surveys which completely covered the territory. Occupancy of territories by single birds was assumed if an additional occupant was not found after (1) at least 1 daytime visit where mice were fed to the occupant and (2) at least 4 additional night-time surveys of the territory.

Capture

Owls were captured and marked after their reproductive status had been determined. Several capture techniques were used, including a snare pole, noose pole (Forsman 1983), baited mist net, dip net and, occasionally, by hand. Handling of captured owls was usually less than 20 minutes. Locking aluminum bands provided by the U.S. Fish and Wildlife Service (USFWS) were placed on the tarso-metatarsus of each captured spotted owl to verify the identity of individual owls during recaptures. Colored plastic leg bands were modified with colored vinyl tabs and placed on the opposing tarso-metatarsus in order to identify individuals without recapturing (Forsman et al. 1996).

Identifying individual owls marked with only USFWS leg bands in previous years required recapturing to check band numbers. Loss of USFWS leg bands was assumed to be zero. The identity of owls detected at night was either inferred by the position of the owl relative to known spotted owl territories or by sight identification of color-marked individuals.

Determining Sex and Age

The sexes of adult and subadult spotted owls were distinguished by calls and general behavior. Males emit lower-pitched calls than females (Forsman et al. 1984). However, fledglings could not be accurately sexed until 1992 when we used examination of sex chromosomes in blood samples to determine juvenile sex (Dvořák et al. 1992, Fleming et al. 1996). Blood samples taken from juveniles were analyzed by Zoogen, Inc. (Davis, California).

spotted owls were aged by plumage characteristics (Forsman 1981, Moen et al. 1991). Four age -classes were used: juvenile (J; fledged young of the year); first-year subadults (S1; one year old); second-year subadult (S2; two years old) and adults (A; at least 3 years old). We could not differentiate age beyond the adult age-class.

Data Analysis

Direct inferences from analysis of our data can, at most, be extended to the resident, territorial population of owls on public lands within the scope of the RSA and, at the least, to specific spotted owl sites sampled within the RSA because selection of study areas and spotted owl sites within the RSA were not random. In both cases, valid inferences are limited to the years when data were collected.

Reproduction. --We defined *reproductive output* as the number of young fledged per spotted owl pair, *productivity* as the number of fledged young per pair producing young and *fecundity* as the number of young fledged of a given sex by a parent of the same sex (e.g., female young fledged per female; Franklin 1992). Trends in reproductive output and productivity were examined using mixed-effects (random effects) models where age was considered a fixed effect, and both year and northern spotted owl territories were considered random effects. We used PROC MIXED in program SAS (SAS Institute 1997) to perform analyses. Models were examined for both time trends and age effects with inferences limited to the portion of the population that were paired (i.e., single birds were not included). We used a log-linear variance structure for the error covariance matrix (Littell et al. 1996:295) because the annual variances of mean number of young fledged was proportional to the mean (Franklin et al. 1990b, 1999a, 2000). A version of Akaike's Information Criterion corrected for sample size (AICc; Hurvich and Tsai 1995) was used for model selection where minimum AICc values indicated the best approximating model for the data. We obtained maximum likelihood estimates of annual reproductive output and productivity using a random effects means model with the ESTIMATE statement in SAS (Littell et al. 1996:141). This model also provided estimates of temporal process variation ($\sigma^2_{temporal}$) from which sampling variation had been removed.

We tested for a 1:1 sex ratio using Fisher's Exact Test (Sokal and Rohlf 1981) in fledged young of known sex where sex was determined by chromosomal analysis of blood samples. Differences in proportions estimated for reproductive activity were tested using chi-square tests of homogeneity (Sokal and Rohlf 1981:724; Zar 1984:49) on the raw counts used to calculate the proportions.

Survival. --We examined mark-recapture data for goodness-of-fit to the global Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965) using program RELEASE (Burnham et al. 1987). We estimated overdispersion (c) by dividing the χ^2 value from TEST2+TEST3 by the degrees of freedom (Burnham et al. 1987). The estimate of c was used to correct for any violations of assumptions that resulted in overdispersion (see Franklin et al. 1999a for details). In previous reports, we used a parametric bootstrap algorithm (White and Burnham 1999). However, further simulations suggested that this algorithm underestimated c.

We used a random-effects modeling approach (Burnham and White 2002) to examine trends in survival of non-juvenile territory holders (S1, S2, and A age-classes). We included the S1, S2, and A portion of capture histories for birds initially captured as juveniles and later recaptured. We modeled survival probabilities using model nomenclature, and selection outlined in Lebreton et al. (1992). We used the model selection approach based on QAICc (see Lebreton et al. 1990, Franklin et al. 1996, Franklin et al. 1999a) that incorporated $\hat{c}$. ΔQAICc and Akaike weights were used to evaluate the degree to which different models were competitive (Burnham and Anderson 1998). We initially examined time-specific models $\{\varphi_t, p_t\}$, $\{\varphi_{a*t}, p_{a*t}\}$, $\{\varphi_{s*t}, p_{s*t}\}$, and $\{\varphi_{a*s*t}, p_{a*s*t}\}$, selecting the most appropriate model from this set using lowest QAICc. We

Table 1. *Annual number of surveys for northern spotted owls conducted in northwestern California, from 1985 through 2001.*

	Survey Type			
Year	Point	Walk-in	Cruise	Total
1985	521	149	36	706
1986	318	156	20	494
1987	726	219	161	1106
1988	1067	212	107	1386
1989	1387	215	89	1691
1990	1425	199	64	1688
1991	1305	244	84	1633
1992	904	207	55	1166
1993	934	170	104	1208
1994	1020	242	96	1358
1995	1129	202	132	1463
1996	1172	249	123	1546
1997	861	224	107	1192
1998	965	216	113	1294
1999	968	170	120	1258
2000	1129	183	127	1439
2001	1031	228	114	1373
Total	16862	3485	1652	22001

then used the annual estimates from the selected time-specific model as the basis for examining trends over time using random effects models (see Franklin et al. 2002). We examined 4 types of trends over time; a linear trend (φ_T), a log-linear trend (φ_{lnT}), a quadratic trend (φ_{TT}), and no trend (a means model, φ.). The random effects models were implemented directly in program MARK (White and Burnham 1999).

Population trends. --We examined population trends by estimating the finite rate of population change (λ) directly from the mark-recapture data from the WCSA using the reparameterized Jolly-Seber estimator (Pradel 1996, Nichols and Hines 2002). This avoided the potential biases in estimating λ from the modified stage-based Leslie matrix that we had used previously. The predominant bias in estimating λ from the Leslie matrix approach was the negative bias in estimates of juvenile survival obtained from mark-recapture estimators. Estimates of λ were a function of apparent survival (accounting for death and emmigration) and recruitment (accounting for local births and immigration). Thus, estimates of λ represented the change in the WCSA population on an annual basis. We used a random effects approach similar to that used for estimating trends in survival, with the model $\{\varphi_t, p_t, \lambda_t\}$ providing annual estimates for the random effects models. We eliminated the first two years of the study (1985 and 1986) in the random effects models because of a potential learning effect by observers that could bias estimates of λ (Hines and Nichols 2002). The last estimate of λ (2000-2001) was not estimable in model $\{\varphi_t, p_t, \lambda_t\}$ because of confounding. Therefore, we were only able examine estimates from 1987-88 through 1999-2000. We used program MARK to perform the analyses (see Franklin 2002).

RESULTS

Surveys

Over 1300 surveys were conducted within our study areas in 2001 (Table 1); 24.9% of these were daytime surveys. Ninety-four territories previously occupied by northern spotted owls were surveyed on the RSA and WCSA in 2001 (Table 2, Figure 1). Owls were detected at 63 (67.0%) and reproduction was assessed at 61 (64.9%) of the territories surveyed (Table 2). We assumed that 31 (33.0%) of the territories were unoccupied. We identified (captured, recaptured

Table 2. *Number of northern spotted owl territories surveyed, occupied and checked for reproduction in 2001 in northwestern California.*

	Study Area		
No. Territories	WCSA	RSA	Combined
Surveyed	56	38	94
With Unknown Status	0	0	0
Assumed Unoccupied	25	6	31
Found Occupied By:			
Pairs	28	27	55
Males	2	4	6
Females	1	1	2
Total	31	32	63
Checked For Reproduction Where Occupied By:			
Pairs	27	26	53
Males	2	4	6
Females	1	1	2
Total	30	31	61

or resighted) 164 individual owls in 2001 (Table 3). We found a total of 51 juvenile spotted owls that had fledged; 27 on the WCSA and 24 on the RSA. All juveniles found were captured and banded. A total of 2,581 identifications of individuals have been made on the WCSA and RSA from 1985 through 2001 (Table 3), not including multiple recaptures and re-sightings of individuals within the same year.

Sex and Age-Class Distribution

The age-class distribution for northern spotted owls between sexes was not different (Fisher's Exact $P = 0.43$). Overall, of the 164 owls found which were identified to age-class and sex, 4.8% were subadults (Table 4) when juveniles were included as an age-class. If juveniles were excluded, subadults were 7.1% of the adult/subadult age-classes. Of the 343 juveniles sexed from 1992 through 2001, 165 were females and 178 were males. There was no apparent deviation from a 1:1 sex ratio among the 10 years (Fisher's Exact $P = 0.58$) although males seemed to predominate, especially in 1996 (35 males, 20 females).

Reproduction

Reproductive activity.— The proportion of pairs checked annually for reproduction which nested from 1985 through 2001 (Table 5) were different among years ($\chi^2 = 84.0$, 16 df, $P < 0.001$). We used only those pairs checked for reproduction before 31 May, which we considered the end of the nesting period. The years 1993, 1995, and 1999 were responsible for the difference ($\chi^2 = 22.9$, 1 df, $P < 0.001$ when 1993, 1995, 1999 tested against the other years combined). When data for 1993, 1995, and 1999 were omitted, the remaining years were not different ($\chi^2 = 12.5$, 13 df, $P = 0.49$). Overall, 52.4% of the pairs nested on average over the 17 years of study (Table 5).

Table 3. *Number of northern spotted owls identified in northwestern California from 1985 through 2001. New birds were owls that had not been previously banded; old birds were owls that had been previously banded.*

	No. new birds captured as:			No. old birds which were:			
Year	Adult & Subadult	Juvenile	Total	Recaptured	Resighted	Total	Grand Total
1985	54	16	70	22	0	22	92
1986	8	17	25	55	0	55	80
1987	48	31	79	42	18	60	139
1988	18	36	54	13	86	99	153
1989	26	39	65	21	87	108	173
1990	25	35	60	14	104	118	178
1991	24	37	61	28	87	115	176
1992	20	49	69	12	114	126	195
1993	12	9	21	13	105	118	139
1994	9	48	57	19	105	124	181
1995	21	15	36	22	83	105	141
1996	11	58	69	17	95	112	181
1997	11	43	54	7	105	112	166
1998	12	32	44	16	93	109	153
1999	17	11	28	10	87	97	125
2000	13	39	52	7	86	93	145
2001	17	51	68	11	85	96	164
Total	346	566	912	329	1340	1669	2581

The proportion of pairs which nested and subsequently fledged young for 1985 through 2001 (Table 5) was also different among years ($\chi^2 = 30.5$, 16 df, $P = 0.02$). Based on cell contributions to the overall χ^2 value, the years 1992 and 2001 contributed most to the difference ($\chi^2 = 5.8$, 1 df, $P = 0.02$ when 1992 and 2001 were tested against the other years combined). When data for 1992 and 2001 were omitted, the data did not support differences between years ($\chi^2 = 15.9$, 14 df, $P = 0.32$). Overall, the proportion of nesting pairs which fledged young on both study areas was 77.6% for the 17 years. This can be considered a crude measure of nest success.

Table 4. *Age-class distribution, by sex, in 2001 for northern spotted owls in northwestern California. The number observed is represented by n and the proportion of each age-class within sex by p.*

	Male		Female		Both Sexes	
Age-Class	n	p	n	p	n	p
Adult	56	0.66	49	0.63	105	0.64
2nd-yr Subadult	0	0.00	1	0.01	1	0.01
1st-yr Subadult	2	0.02	5	0.06	7	0.04
Juvenile	27	0.32	24	0.30	51	0.31

The proportion of pairs checked which fledged young from 1985 through 2001 (Table 5) was different among years ($\chi^2 = 71.2$, 16 df, $P < 0.001$). Again, this difference was attributed to years 1993, 1995, and 1999 ($\chi^2 = 15.0$, 1 df, $P < 0.001$ when 1993, 1995, and 1999 were tested against the other years combined; $\chi^2 = 13.8$, 13 df, $P = 0.39$ when 1993, 1995, and 1999 were omitted from the analysis). For the 17 years

Table 5. *Proportion of northern spotted owl pairs checked for reproductive activity (n) which nested, which nested and successfully fledged young, and which fledged young in northwestern California from 1985 through 2001. Standard errors are in parentheses.*

	Proportion of pairs which:					
	Nested		Nested and fledged young		Fledged Young	
Year	n[a]	proportion	n[b]	proportion	n[c]	proportion
1985	33	0.49 (0.087)	16	0.81 (0.098)	42	045 (0.077)
1986	25	0.64 (0.096)	16	0.56 (0.124)	37	0.38 (0.080)
1987	31	0.65 (0.086)	20	0.70 (0.102)	57	0.42 (0.065)
1988	36	0.64 (0.080)	23	0.87 (0.070)	62	0.47 (0.063)
1989	52	0.60 (0.068)	31	0.74 (0.078)	65	0.42 (0.061)
1990	53	0.66 (0.065)	35	0.63 (0.082)	67	0.40 (0.060)
1991	58	0.64 (0.063)	37	0.70 (0.075)	67	0.42 (0.060)
1992	49	0.45 (0.071)	22	1.00 (0.000)	74	0.42 (0.057)
1993	25	0.16 (0.073)	4	0.75 (0.217)	59	0.10 (0.039)
1994	50	0.62 (0.069)	31	0.68 (0.084)	62	0.44 (0.063)
1995	49	0.16 (0.053)	8	0.88 (0.117)	59	0.19 (0.051)
1996	40	0.70 (0.072)	28	0.93 (0.049)	57	0.65 (0.063)
1997	49	0.55 (0.071)	27	0.81 (0.075)	61	0.46 (0.064)
1998	51	0.59 (0.069)	30	0.73 (0.075)	56	0.43 (0.066)
1999	42	0.17 (0.058)	7	0.86 (0.132)	54	0.15 (0.048)
2000	41	0.61 (0.076)	25	0.76 (0.085)	52	0.46 (0.069)
2001	39	0.49 (0.080)	19	1.00 (0.000)	53	0.55 (0.068)
Overall[d]	723	0.49 (0.019)	379	0.78 (0.021)	984	0.40 (0.016)

[a]Total number of pairs checked each year before 31 May.
[b]Total number of nesting pairs found each year before 31 May.
[c]Total number of pairs checked throughout the entire sampling period in each year.
[d]estimate represents overall outcomes rather than pairs because same pairs often measured across years.

combined, 39.9% of the pairs checked successfully fledged young.

Reproductive output.— We modeled reproductive output using two data sets: one which included all pairs, including those whose members were of an unknown age-class, and one which included only pairs where females were of known age-class. We used the analysis from the first data set to compare reproductive output with reproductive activity in terms of time trends and the analyses from the second data set ultimately to estimate age-specific and sex-specific fecundity rates.

Using data on pairs only (regardless of whether both members had been aged), we analyzed 5 mixed-effects models. In these models, we examined the data for variable time trends (model R_t), linear time trends (model R_T), no time trends (model R .), quadratic time trends (R_{T+T^2}), time trends with a threshold (R_{lnT}), and for "good" and "bad" years represented as a categorical variable (model R_g). The latter model was based, a priori, on observations of low reproduction in 1993, 1995, and 1999 which were categorized as "bad" years with the other years categorized as "good" years. Based on minimum AICc, model R_g was selected (AICc = 2397.46,

Table 6. *Mean productivity and mean number of young fledged per pair for northern spotted owl pairs in northwestern California, from 1985 through 2001. Means represent least square means from random-effects means model for productivity and reproductive output. Pairs are number of pairs checks for reproductive activity.*

	Productivity			No. young fledged per pair		
Year	Pairs	Mean	SE	Pairs	Mean	SE
1985	19	1.693	0.091	42	0.749	0.125
1986	14	1.583	0.095	37	0.602	0.117
1987	24	1.672	0.077	57	0.699	0.107
1988	29	1.490	0.083	62	0.653	0.093
1989	27	1.676	0.087	65	0.701	0.105
1990	27	1.475	0.078	67	0.572	0.085
1991	28	1.484	0.078	67	0.600	0.088
1992	31	1.700	0.069	74	0.709	0.096
1993	6	1.568	0.113	59	0.186	0.062
1994	27	1.758	0.067	62	0.752	0.107
1995	11	1.533	0.101	59	0.304	0.076
1996	37	1.659	0.080	57	0.991	0.111
1997	28	1.583	0.078	61	0.700	0.101
1998	25	1.418	0.077	56	0.574	0.091
1999	8	1.529	0.109	54	0.240	0.070
2000	24	1.638	0.079	54	0.735	0.110

$K = 21$ parameters). This model was heavily weighted (Akaike weight = 1.00) indicating that none of the other models explained the variation in the data as well as model R_g. Estimates of the number of young fledged per pair from model R_g were 0.198 (SE = 0.044) for years 1993, 1995, and 1999 combined ("bad" years) and 0.707 (SE = 0.033) for the other years combined ("good" years). Annual estimates for reproductive output for pairs are shown in Table 6 for comparison.

To estimate reproductive output for females, we used data for individuals of known age-class only. We examined 32 random-effects models which included combinations of time and age effects, and their interactions. Of these 32 models, model ($R_{g*[fS1,fS2,fA]}$) was selected as the best model (AICc = 2245.33, $K = 26$, Akaike weight = 0.862). This model had separate estimates for S1, S2 and adult females which varied differently between "good" and "bad" (1993, 1995, and 1999) years. The next closest model ($R_{g+[fS1,fS2,fA]}$, Akaike weight = 0.108) was not a competitive model because of its low weighting. This model suggested a similar relationship as the selected model except it lacked an interaction between the age-classes and good and bad years. The remaining models were not competitive with Akaike weights <0.04. Estimates of reproductive output in "good" and "bad" years for each age-class are shown in Figure 2. These estimates suggested that adults had better reproductive output than subadults during "good" years but this advantage decreased considerably during "bad" years. These results were similar to those reported in previous years. Based on a random-effects means model, northern spotted owl

Table 7. Mean estimates, standard errors (SE) and process standard deviation ($\hat{\sigma}_{temporal}$) of reproductive output (R), productivity (P), survival (φ), and rates of population change (λ) for northern spotted owls in northwestern California from 1985 through 2001. Estimates are from random effects means models.

Parameter	Mean	SE	$\hat{\sigma}_{temporal}$	$CV_{temporal}$
R	0.637	0.064	0.230	0.361
P	1.605	0.042	0.128	0.080
φ	0.864	0.013	0.028	0.032
λ	0.980	0.016	0.000	0.000

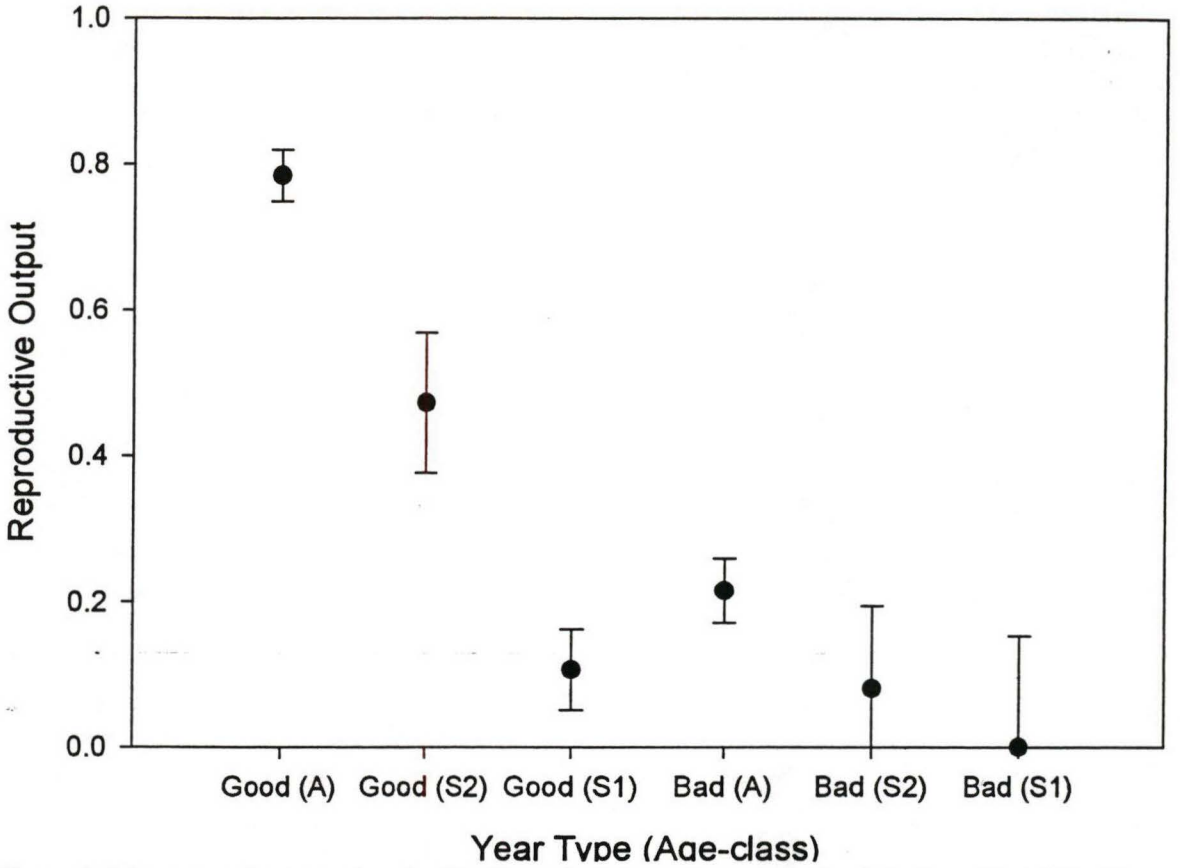

Figure 2. *Mean reproductive output for S1 , S2, and adult northern spotted owls in "good" and "bad" years in northwestern California. Bars are one standard error from the mean.*

pairs of known age fledged an average of 0.637 young per year (Table 7). This parameter had fairly substantial annual variation, based on the coefficient of temporal process variation ($CV_{temporal}$; Table 7). The model ($R_{g*[fS1,fS2,fA]}$) explained 100% of this process variation.

We investigated effects on productivity in pairs and individuals of known age with 32 mixed-effects models similar to those used to describe reproductive output. The model selected (P_g; AICc = 606.26, K = 21, Akaike weight = 0.213) suggested that productivity was also affected by "good" and "bad" years. Model P_{lnT} and P_T were competitive models (Akaike weights = 0.101 and 0.082, respectively) that suggested weak log-linear and linear time trends in productivity. Under model P_g, productivity was higher in "good" years (1.625, SE = 0.042) than in "bad" years (1.436, SE = 0.123). The lack of precision in the estimates of productivity for the "bad" years indicated that the "good" versus "bad"year effect was weak. In addition, the parameter estimate for this effect ($\hat{\beta}_1$ = 0.188, SE = 0.130, 95% CI = -0.067, 0.443) was imprecise and the variation explained by the model was only 12.8%. The uncertainty in model selection was primarily due to lack of trends and relatively low process variation in the annual estimates (Table 7). Based on a random-effects means model, northern spotted owl pairs of known age that fledged young fledged an average of 1.61 young per year (Table 7). This parameter exhibited little annual variation, relative to reproductive output, based on the

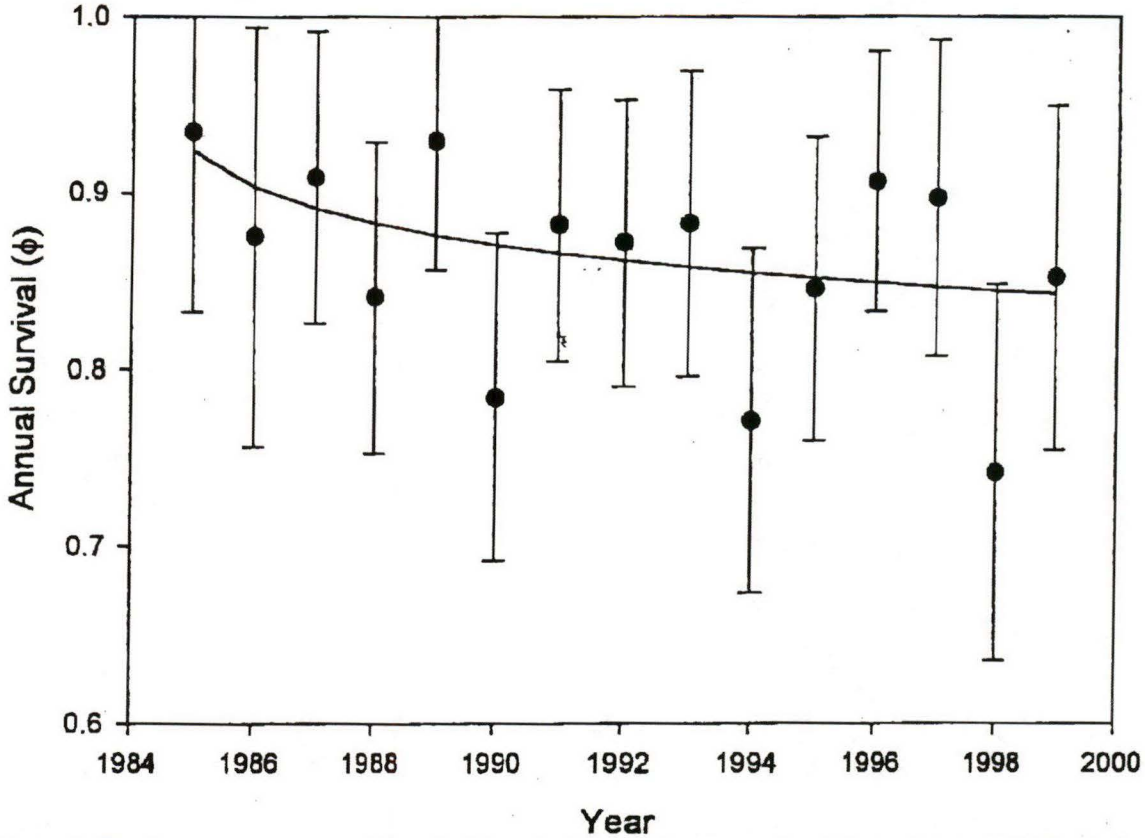

Figure 3. *Trends in apparent survival for subadult and adult northern spotted owls in northwestern California from 1985 through 2001. Trend estimates were from random effects model* $\{\varphi_{lnT}\}$. *Estimates of individual values (solid dots)* ± *95% confidence limits are from model* $\{\varphi_t, p_t\}$ *for comparison. The estimate for 2000-2001 was not estimable.*

coefficient of temporal process variation (Table 7). Annual estimates are shown in Table 6 for comparison.

Annual Survival

We modeled the survival of territory holders using data partitioned by sex and the three age-classes (S1, S2 and A). Based on the goodness-of-fit, the global mark-recapture model $\{\varphi_{a*s*t}p_{a*s*t}\}$ exhibited overdispersion ($\hat{c}$ = 1.70; χ^2 for TEST2+TEST2 = 329.43, 194 df). We incorporated this estimate into the modeling procedure to adjust estimates for overdispersion. We initially examined 6 models that included combinations of age-class, sex and time effects with no constraints on time (e.g., φ and p always varied by year, t). From this initial set of models, model (φ_t, p_t) best approximated the data. The last estimates of φ (for the interval 2000-2001) and p (for 2001) were confounded and therefore not estimable. We then used the annual estimates from this model for the random effects modeling process. Three competitive models resulted from the random effects modeling process: $\{\varphi_{lnT}\}$ (Akaike weight = 0.356), $\{\varphi_T\}$ (Akaike weight = 0.290), and $\{\varphi .\}$ (Akaike weight = 0.209). The log-linear trend for the best approximating model $\{\varphi_{lnT}\}$

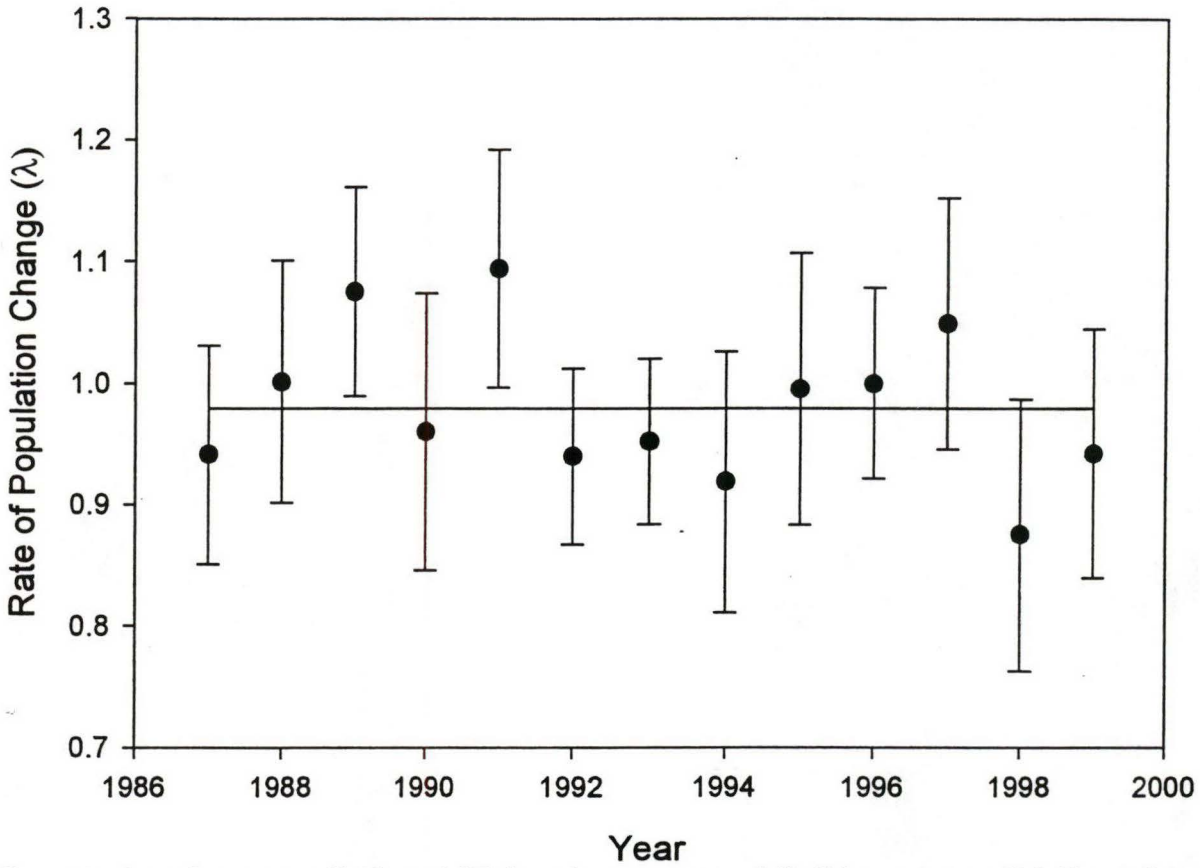

Figure 4. *Annual estimates of λ (dots ± 1 SE) from the reverse-time Jolly-Seber estimator. Solid line indicates estimate from random effects model {λ .}.*

was negative (β_1 = -0.030, SE = 0.019, 95% CI = -0.067, 0.007), which suggested that annual survival for territory holders declined and then stabilized (Figure 3). However, this trend was not strongly supported by the data because of the imprecision of the slope parameter and the model explained only 43.9% of the variation (see also Figure 3). Based on the random-effects means model, annual apparent survival for territory holders averaged 0.864 which did not vary substantially from year to year (Table 7).

Population Trends

We used annual estimates for λ from the reverse-time Jolly-Seber model $\{\varphi_t, p_t, \lambda_t\}$ to estimate trends in λ over time on the WCSA, using the random effects models. We first assessed the global model $\{\varphi_t, p_t, \lambda_t\}$ for goodness of fit using program RELEASE and computed an estimate of overdispersion of $\hat{c}$ = 1.75 that was used to correct AIC and standard errors. Of the 4 random effects models examined, model {λ .} was selected as the best approximating model based on QAICc (Akaike weight = 0.590), and suggested that λ was fairly constant over time. Model $\{\lambda_{lnT}\}$ was the second-ranked model (Akaike weight = 0.229). Model $\{\lambda_{lnT}\}$ would have been considered a competitive model except that the deviance for this model was the same as for model {λ .}. Thus, the difference in AIC between the two models (ΔQAICc = 1.94} was due to

the addition of an extra parameter that contributed little in explaining the variation in the data. Thus, we concluded that the data could not support a time trend in λ (Figure 4). This was supported by the lack of estimable temporal process variation (Table 7). The estimate of λ from 1985 through the interval 1999-2000 (the interval 2000-2001 was not estimable using random effects models) on the WCSA was 0.980 (SE = 0.016), which was not different from $\lambda = 1$ (a stationary population) based on 95% confidence intervals (0.949, 1.011).

DISCUSSION

We used a different approach in examining trends in population parameters, concentrating on the use of random effects models rather than fixed effects models, as was done in past reports. The use of random effects models is a more conservative approach in detecting trends because the sampling unit, in our case, is year rather than bird or territory. Thus, standard errors for slope parameters are larger than with fixed-effect models. However, inferences are still confined to the period of study (Franklin et al. 2002). We believe the random effects approach is a useful way to examine trends in our data (see Burnham and White 2002).

Reproduction in northern spotted owls on our study area continues to follow the pattern of low reproductive output in "bad" years and average or, occasionally, high reproductive output in "good" years. Reproduction is the most variable parameter in our study population. We have had three years (1993, 1995, and 1999; Table 6) of very low reproduction which are probably most responsible for this variation. The low reproductive output in 1999 has been followed by two years of average and above average reproductive output. While productivity and the proportion of nests that fledge young have remained relatively stable, the proportion of birds nesting each year are primarily responsible for the low reproductive output. That is, very few birds nested in 1993, 1995 and 1999, which was primarily responsible for low reproductive output in those years.

The presence of trends in annual survival of territory holders was weakly supported. Rather, the variation in annual survival is probably better supported by inclusion of environmental covariates, such as weather (see Franklin et al. 2000). We were unable to estimate survival from 2000 to 2001 using the random effects approach because of confounding between the last estimates of φ and p in the mark-recapture estimators. We have had three years of below average apparent survival, 1990-1991, 1994-1995, and 1998-1999 (Figure 3). Two of these periods correspond to years that also had low reproductive output. These "catastrophic" events of years with both low survival and low reporductive output seem to be increasing since the inception of the study. We are still exploring the effects of increased frequency of El Niño climatic events as one factor explaining these events.

The average rate of population change for the WCSA population was not different from a stationary population ($\lambda = 1$). We were unable to estimate any temporal process varaition from these estimates because annual sampling variation was large. However, the annual estimates suggested that there were periods when the population declined followed by periods of increase (Figure 4). We are currently exploring ways to include the RSA in this estimator to reduce sampling variation. The primary problem with including data from the RSA is that the RSA are clusters of territories whereas the WCSA is a large defined unit that is consistently sampled. An important distinction between the inference from λ derived from the reparameterized Jolly-Seber

estimator and λ derived from the Leslie matrix is that the reparameterized Jolly-Seber λ addresses the question "have the territorial females been replaced?" rather than "have the territorial females replaced themselves?" (Franklin et al. 1999a). Thus, a population with a stationary λ estimated using the reverse-time Jolly-Seber approach could be a self-sustaining population, one that is maintained solely from outside immigration, or a combination of both. Thus, it is possible for a population to be declining demographically while being numerically stable because of emigration (i.e., a sink population, sensu Pulliam 1988). We anticipate that analytical techniques will be available shortly that will allow us to estimate *in situ* recruitment from outside immigration; this will better allow us to determine the status of our study population.

We believe that estimates of rates of population change for northern spotted owls that are based solely on the Leslie-matrix approach do not provide a complete or accurate picture of the dynamics of this population. For example, we continue to believe that survival rates estimated from banded juveniles are negatively biased because of the dispersal ability of juveniles (Gutiérrez et al. 1985, Miller 1989). If juveniles permanently emigrate from our study areas and survive at least one year, then our estimates of juvenile survival will be biased low. We are still working on estimating juvenile emigration rates from our study areas using mark-recapture estimators. Regardless, we will continue to use the alternative method for estimating population rates of change.

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